Organic matter bioavailability in tropical coastal waters: the Great Barrier Reef

Christian Lønborg[1*], Xosé Antón Álvarez–Salgado[2], Samantha Duggan[1] & Cátia Carreira[3]

[1]Australian Institute of Marine Science, PMB No 3, Townsville, Queensland 4810, Australia

[2] IIM-CSIC, Instituto de Investigacións Mariñas, Eduardo Cabello 6, 36208 Vigo, Spain

[3]Departamento de Biologia and CESAM, Universidade de Aveiro, Campus Universitario de Santiago, Aveiro 3810-193, Portugal

[*]Corresponding author:
Australian Institute of Marine Science
PMB 3, Townsville MC, QLD 4810
Australia
Phone: 0061 (0) 7 4753 4382
Fax: 0061 (0) 7 4772 5852
Email: c.lonborg@aims.gov.au; clonborg@gmail.com

Running head: Great Barrier Reef organic matter degradation

Keywords: particulate organic matter, dissolved organic matter, stoichiometry, bioavailability, degradation rate constants, Great Barrier Reef

Abstract

Bioavailability of organic matter in tropical coastal ecosystems, and particularly in coral reefs, is largely unknown. In order to ameliorate this gap, we collected samples at three locations during the dry and wet seasons in the Great Barrier Reef and measured changes in particulate (POM) and dissolved (DOM) organic matter concentrations in dark, temperature controlled (22–24ºC), laboratory incubations over 50 days. This allowed determining the bioavailable fractions, stoichiometry and degradation rate constants for both pools. The sites did not show any difference in salinity and therefore, observed differences could be related to factors such as disparities in the biological activity and/or the impact of sediment resuspension rather than to location. Our results demonstrate that 58 ± 8 % of particulate (POC) and 16 ± 5 % of dissolved organic carbon (DOC) is bioavailable. These proportions increase when the N (particulate: 75 ± 5 %; dissolved: 32 ± 4 %) or P (particulate: 90 ± 3 %; dissolved: 68 ± 8%) pools are examined, suggesting that compounds containing C, N and P are more reactive than compounds containing only C and N, which in turn are more labile than compounds containing just C for both pools. This trend is also confirmed by the degradation rates. Furthermore, our results demonstrate that 94% and 75% of the bioavailable N and P are contained in the organic fraction and that these are able to deliver enough nutrients to sustain phytoplankton productivity in the Great Barrier Reef. Our results emphasise that organic matter is a key and mostly unaccounted part of the C, N and P cycles in tropical coastal waters of the Great Barrier Reef.

Introduction

Organic matter (OM) plays a key role in the cycling of carbon, nitrogen and phosphorus in marine systems in general and in the coastal ocean in particular (Hedges 2002). OM is a highly complex mixture (Repeta 2015), typically divided, in aquatic systems, into the material that is retained on a filter with a pore size between 0.2 and 0.7 μm (particulate organic matter; POM) or passes the filter (dissolved organic matter; DOM). This division is purely operational (Verdugo 2012), but the distinction has implications from the view point of biogeochemical cycles: POM can sink to the sediments while DOM remains in the water column. The POM pool consists of a minor fraction of living biomass (e.g. bacteria, zooplankton) and a major fraction of detritus (e.g. dead cells, faecal pellets), while the DOM pool is mainly lifeless (Hedges 2002). On average DOM concentrations are 1 to 2 orders of magnitude greater than that of POM in coastal waters (Barrón and Duarte 2015).

Coastal waters are amongst the most productive and biogeochemically active zones of the marine biosphere, responsible for 14–33% of total oceanic production and approximately 80% of organic matter burial (Gattuso et al. 1998). In these waters, OM originates from either autochthonous or allochthonous sources. The autochthonous OM sources are: plankton organisms (Møller 2004; Nagata and Kirchman 1992), macroalgae (Wada et al. 2008), macrophytes (Søndergaard 1981), sediments (Burdige et al. 2004) and even fish (Dundas 1985). The main allochthonous sources include: atmospheric dry and wet deposition (Jickells et al. 2013; Kieber et al. 2006), submarine groundwater discharge (Santos et al. 2012), rivers, streams and overland flow (Meybeck 1982). Four processes have been identified to remove OM from the water column in coastal waters: 1) biological utilization (e.g., Lønborg et al. 2009b); 2) photochemical reactions, where OM is either transformed into recalcitrant compounds (e.g., Kieber et al. 1997), degraded directly to carbon monoxide or dioxide, or to simpler compounds more bioavailable for bacterial uptake (e.g., Mayer et al. 2011); 3) loss

via aggregation and sorption leading to sedimentation (Burd and Jackson 2009; Carlson et al. 1985); and 4) abiotic degradation via free radical reactions of OM with oxygen (Rontani et al. 2014). In general, it is assumed that the POM fraction is less degraded and more bioavailable than the DOM pool, but both contain labile compounds with short turnover times (from hours to days), a semi-labile pool with longer turnover times (from weeks to months) and a recalcitrant background pool (Boudreau and Ruddick 1991; Hansell 2013).

Previous studies have shown that both autochthonous and allochthonous OM can be degraded by marine bacteria, with the bioavailability depending on an array of factors including molecular size and structure, environmental conditions such as inorganic nutrient limitation of bacterial activity, redox state, microbial community composition and mineral associations, or extreme dilution of individual molecules (Amon and Benner 1996; Benner and Opsahl 2001; Dittmar 2015; Keil and Mayer 2014; Moran et al. 1999; Thingstad et al. 1999).

Tropical coastal waters harbour some of the most complex and productive ecosystems on Earth, including coral reefs. They receive approximately one order of magnitude more inputs of continental carbon, nitrogen and phosphorus than temperate and artic regions (Brunskill 2010). Phytoplankton production rates in tropical continental shelves and estuaries have also been shown to match some of the most productive areas of the global ocean (i.e. upwelling areas). These high rates have been supported by elevated temperatures and a steady supply of nutrients and solar radiation (Nittrouer et al. 1995). The fate of the terrestrial material, *in situ* mineralization *versus* export to the adjacent ocean, depends on erosional and morphological issues. Mineralization is favoured in low erosional river catchments combined with narrow shelves. The Amazon and the Ganges-Brahmaputra catchment areas are extreme cases of low and highly erosional basins that derive in predominant mineralization (Medeiros et al. 2015) and preservation (Galy et al. 2015) of terrestrial OM, respectively. Furthermore, in tropical

92 coastal systems with a narrow shelf, such as the coastal waters of the Bismarck Sea, most of
93 the terrestrial material is, together with the OM produced in situ, exported to the open ocean
94 (Brunskill 2010; Burns et al. 2008). On the contrary, in broad shelves, such as the Great
95 Barrier Reef, almost all OM is degraded within the continental shelf (Brunskill et al. 2010).
96 Despite that these coastal systems are productive and important to both regional and global
97 biogeochemical cycles and food webs, few studies have investigated the microbial
98 bioavailability and degradation of both POM and DOM in the water column of tropical
99 coastal waters (Medeiros et al. 2015; Ward et al. 2013) and there is therefore still a lack of
100 mechanistic understanding of which factors influences the OM degradation.
101 In this work we present results from experiments designed to: 1) quantify the seasonal
102 bioavailability of POM and DOM; 2) estimate the POM and DOM stoichiometry during
103 microbial degradation; and 3) determined the POM and DOM degradation rate constants
104 using laboratory incubations in the Great Barrier Reef, Australia.
105
106 ***Methods***
107 **Study area**
108 The Great Barrier Reef (GBR) is situated on the continental shelf and slope of Australia's
109 northeast coast. The GBR has a maximum width of 330 km and extents over an area of
110 344,000 km^2 (Fig. 1). Approximately 7% of this area is covered by corals (total of ~3700
111 reefs) which are primarily located at distance, ranging from ~ 15 to 150 km, from shore; with
112 the open water body separating the reef from the mainland known as the GBR lagoon. This
113 lagoon has a water depth of around 10-20 m close to shore increasing to 40 m towards the
114 reefs, representing an area of around 238,700 km^2. Within the central part of the lagoon,
115 currents are primarily equatorward, driven by the predominant south-easterly trade wind

116 regime from March through October, and winds are more variable during the austral summer
117 (Wolanski 1994).
118 Over the continental slope, the East Australian Current (EAC) flows poleward and enters
119 onto the shelf and outer lagoon by passages between reefs (Fig. 1). The combined effect of
120 currents, tidal mixing and winds does that surface waters of the GBR lagoon are normally
121 well mixed exhibiting very little stratification. The GBR region has a monsoonal climate,
122 characterized by a wet summer (December–March) season and a dry winter season, with
123 around 60% of the annual rainfall occurring in the wet season.
124 Plankton communities in the GBR are in nearshore waters frequently dominated by diatoms,
125 while further offshore picoplankton unicellular cyanobacteria (*Synechococcus*) and
126 prochlorophytes (*Prochlorococcus*) dominate, together with N_2-fixing cyanobacteria
127 (*Trichodesmium*) and assemblages of open-ocean dinoflagellates (Furnas et al. 2005;
128 Revelante and Gilmartin 1982). The average plankton primary productivity varies between
129 0.1 and 1.5 g C m^{-2} d^{-1} with highest rates in nearshore waters during the summer wet season,
130 while further offshore no clear seasonal signals are found (Furnas et al. 2005). River inputs
131 together with both surface and upwelled water from the Coral Sea, N_2 fixation and rain
132 represent the largest external source of nutrients to the system (Furnas et al. 2011). As the
133 magnitude of different sources, sinks and cycling of nutrients (both inorganic and organic) in
134 the GBR is poorly understood, it is currently not possible to confidently state which of these
135 sources are the most important at any given time and place. Dissolved organic matter (DOM)
136 contains around 80% of the nitrogen and phosphorus forms; particulate nitrogen and
137 phosphorus represent approximately 19%, while the remaining 1% are contained in the
138 inorganic nutrient pools (Furnas et al. 2011).
139 In this study we determined the bioavailability, stoichiometry and degradation rates of POM
140 and DOM at three stations in the late dry (September 2014), wet (February 2015) and early

dry seasons (June 2015). Fig. 1 shows the three study sites, which all have been sampled frequently over the past 10 years as part of the GBR Marine Monitoring Program (MMP; (Lønborg et al. 2016). These sites were chosen as they are impacted differently by 1) sporadic continental runoff, 2) sediment resuspension events and turbidity levels due to differences in local wind conditions and water depth and 3) upwelled water from the Coral Sea, with sta. 1 and 2 likely being influenced and sta. 3 largely unaffected. The three sites furthermore span across the 20 m bathymetry depth range (sta. 1 – 16 m; sta. 2 – 40 m and sta. 3 – 23 m), with terrigenous materials dominating sediments and suspended matter below this depth and biogenic carbonates at deeper stations (Belperio and Searle 1988).

Sample collection

Meteorological data reported in this study (wind speed and direction) were measured by automatic sensors installed on board the R/V *Cape Ferguson*. Full-depth continuous conductivity-temperature-depth (CTD) profiles were recorded prior to water collection with a Seabird SBE 37 plus at each sampling site. The CTD salinity was calibrated with water samples collected with the Niskin bottles and analysed in the base laboratory with a Portasal Model 8410A. The observed Secchi-disk depth (in m) was measured as the depth at which a lowered white disk (18 cm diameter) just disappears from the observer's sight. The disk was lowered on the lee side of the vessel in order to minimize wind driven surface ripples and where possible on the sunny side of the vessel. Although the disk does not provide an actual quantitative measure of light penetration, it does provide a method to determine limits of visibility for comparative purposes. Water for the laboratory incubation experiments was collected with a 25 L Niskin bottle at 5 m depth, and combined into two 50 L acid washed containers.

Sample water (1 L) for total suspended solids (TSS) analysis was collected on pre-weighed 0.4 μm polycarbonate filters (47 mm diameter). After filtration, filters were rinsed with 50 mL of deionized water to remove salt. TSS concentrations were determined gravimetrically from the mass difference between loaded and unloaded filters after drying overnight at 60°C. Water for chlorophyll *a* (Chl *a*) determination was filtered (between 100 and 200 mL) through GF/F filters (nominal pore size of about 0.7 μm), which were frozen (-20°C) until analysis. Chl *a* was measured with a Turner Designs 10000R fluorometer after 90% acetone extraction (Yentsch and Menzel 1963). Field samples were also collected for the analysis of particulate organic carbon (POC), nitrogen (PN) and phosphorus (PP) and dissolved inorganic nutrients (NH_4^+, NO_3^-/NO_2^- and HPO_4^{2-}). It should be noted that as we do not distinguish between the inorganic and organic part of the particulate nitrogen and phosphorus fractions, we therefore refer in this article to particulate nitrogen (PN) and phosphorus fractions (PP). A volume of 250 mL of sample water was collected under low-vacuum on precombusted GF/F filters for particulate matter and filters were kept frozen (-20°C) until analysis. Dissolved nutrients were immediately filtered through a 0.45 μm filter cartridge (Sartorius MiniSart) into acid-washed 50 mL HDPE plastic containers and kept frozen (-20°C) until analysis.

Experimental design

Filtration of the water for the incubation experiments started within 10 min of collection; one part (45 L of natural seawater) was filtered through a dual-stage (0.8 μm and 0.2 μm) filter cartridge (Pall-Acropak supor Membrane) which had been pre-washed with 10 L of Milli-Q water to isolate the dissolved fraction; a second part (50 L of natural seawater) was used to harvest the suspended particles under low vacuum pressure on 142 mm 0.2 μm filters (Pall, Supor membrane Disc Filter), these were dried and stored at −20 °C after collection until

190 used within 2 hours; and a third part of the sample water (5 L) was filtered through pre-
191 combusted (450°C for 4 h) GF/C filters (nominal pore size of about 1.2 μm), to establish a
192 microbial culture. After filtration, the 0.2 μm filtered seawater was immediately transferred
193 into two 20 L carboy's corresponding to the POM and DOM degradation experiments. For
194 the POM experiment the collected suspended particles from 50 L of seawater were
195 resuspended in the 0.2 μm filtered seawater and the particles were kept homogeneous in
196 suspension during distribution into the incubation containers with a gentle stirring provided
197 by a magnetic stirrer. This was followed by the addition of the microbial inoculum to both
198 experiments, which was added corresponding to 10% of the total volume. The water for each
199 experiment was thereafter distributed into glass bottles (500 mL) and incubated in the dark at
200 a constant temperature of 22-24°C with four replicate bottles being analysed for each sub-
201 sampling at day 0, 2, 4, 12 and 50. Additional bottles for subsampling at day 1 in the POM
202 experiments were collected to follow the soluble part of the DOM and inorganic nutrient
203 pools, which was assumed to be the material released within the first day. During the 50 days
204 incubation period no stirring was applied. All glassware used in the experiments was acid
205 washed (10 % HCl for 24 h) and rinsed with Milli-Q water prior to use. Unfiltered water from
206 the POM experiments were used to follow changes in total organic carbon (TOC), total
207 nitrogen (TN) and phosphorus (TP). Samples for the analysis of the dissolved phase were
208 collected from both experiments by filtration through prewashed (250 mL Milli-Q water) 0.2
209 μm filters (Pall, Supor membrane Disc Filter) to follow dissolved inorganic nitrogen (DIN:
210 NH_4, NO_2^- and NO_3^-) and phosphorus (DIP: HPO_4^{-2}), dissolved organic carbon (DOC), total
211 dissolved nitrogen (TDN) and phosphorus (TDP). Water samples for DIN, DIP, TP and TDP
212 were collected in 20 mL acid washed polyethylene bottles and kept frozen (-20ºC) until
213 analysis. Sub-samples (10 mL) for TOC, DOC, TN and TDN analysis were collected in pre-
214 combusted (450ºC, 12 hours) glass ampoules and preserved by adding 50 μL 25 % H_2PO_4.

215

216 **Sample measurements**

217 Inorganic nutrients (NH_4^+, NO_3^-/NO_2^- and HPO_4^{2-}) were determined by standard segmented
218 flow analysis (Hansen and Koroleff 1999). The precisions were ± 0.01 μmol L^{-1} for NH_4^+, ±
219 0.1 μmol L^{-1} for NO_3^-/NO_2^- and ± 0.02 μmol L^{-1} for HPO_4^{2-}. Field samples for the
220 determination of POC and PN were measured by high temperature combustion (950ºC) using
221 a Shimadzu TOC-V carbon analyser fitted with a SSM-5000A solid sample module, after the
222 inorganic carbon on the filters (e.g. $CaCO_3$) had been removed by acidification of the sample
223 with 2M HCl (Nieuwenhuize et al. 1994). The analyser was calibrated using AR Grade
224 EDTA for the 5 point standard curve. Field concentrations of PP were determined
225 spectrophotometrically as inorganic P after digesting the particulate matter in 5% potassium
226 persulphate. The method was standardised using orthophosphoric acid as the standard for the
227 4 point calibration curve. We compared peak areas of the filter blanks and standard solutions
228 to ensure consistency between runs with no major deviations found. The TOC, DOC, TN and
229 TDN concentrations were measured by high temperature combustion (720ºC) using a
230 Shimadzu TOC-L carbon analyser coupled in series with a nitric oxide chemiluminescence
231 detector. Prior to analysis, CO_2 remaining in the acidified sample water was removed by
232 sparging with O_2 carrier gas. Three to five replicate injections of 150 μL were performed per
233 sample. Concentrations were determined by subtracting a Milli-Q blank and dividing by the
234 slope of a daily 4 points standard curve made from potassium hydrogen phthalate and
235 glycine. To avoid the small error associated with day-to-day instrument variability, all
236 samples from a given experiment were analysed on a single day. Using the deep ocean
237 reference samples we obtained an average concentration of 42.1 ± 0.6 μmol L^{-1} for DOC and
238 31.3 ± 0.4 μmol L^{-1} for TDN (n = 40). The nominal values provided by the reference
239 laboratory (Prof. Hansell Lab) are 41–44 and 32.25–33.75 μmol L^{-1} respectively. DON

concentrations were obtained by subtracting DIN from TDN (DON = TDN – DIN), with the standard error calculated as $SE^2_{DON} = SE^2_{TDN} + SE^2_{DIN}$. TDP and TP were measured in triplicate by oxidation to soluble reactive phosphorous with the addition of sulphuric acid and persulfate (Koroleff 1983), following autoclaving at 100°C for 90 min. DOP was calculated as the difference between TDP and DIP (DOP = TDP – DIP) with the SE for DOP calculated as: $SE^2_{DOP} = SE^2_{TDP} + SE^2_{DIP}$. The time course changes in particulate concentrations in the POM degradation experiments were calculated as the difference between TOC and DOC for POC, TN and TDN for PN, and TP and TDP for PP. The corresponding standard errors were calculated as $SE^2_{POC} = SE^2_{TOC} + SE^2_{DOC}$, $SE^2_{PN} = SE^2_{TN} + SE^2_{TDN}$, and $SE^2_{PP} = SE^2_{TP} + SE^2_{TDP}$, respectively.

The decay of the bioavailable fraction of POM and DOM during the course of the incubations was modelled by a first-order exponential decay function. The unchanging recalcitrant pool was also included in the model. For the POM this was expressed as:

$$POM(t) = BPOM \cdot \exp\left(k_{POM} \cdot t\right) + RPOM \quad (1)$$

and for DOM as:

$$DOM(t) = BDOM \cdot \exp\left(k_{DOM} \cdot t\right) + RDOM \quad (2)$$

Where BPOM and BDOM are the bioavailable pools (in μmol L^{-1}), k_{POM} and k_{DOM} the first-order degradation rate constants (in d^{-1}), t the time (in days) and RPOM and RDOM the remaining pool after 50 days of incubation (in μmol L^{-1}). In this study, the bioavailable pool was defined as the difference between the initial and final concentration. Since the bioavailable and recalcitrant pools are calculated prior to fitting the time evolution of POM and DOM, the only parameter that is adjusted is the degradation rate constant. Note that despite the initial conditions for each degradation experiment were different with respect to abundance of bacteria (varied up to 5 times; data not shown) we did not find any relationship

between degradation rate constants and abundance. Therefore, we assume that the differences were evened out within days.

Statistical analysis

Regression analyses were performed using the best–fit between the two variables X and Y obtained by regression model II (Sokal and Rohlf 1995). In the cases where the intercept was not significantly different from zero, it was set to zero and a new slope was calculated. Prior to regressions, normality was checked and the confidence level was set at 95%, with all statistical analyses conducted in Statistica 6.0. Furthermore, T-Student tests were performed to test the significance of differences in environmental conditions between seasons and stations ((Sokal and Rohlf 1995)). Degradation rate constants for the DOM pool, obtained at 22-24ºC, were normalized to 15ºC to allow comparison with other values reported in the literature. Following Lønborg and Álvarez-Salgado 2012 , $k(15ºC) = k(T)* Q_{10}^{10/(15-T)}$ where k(15ºC) and k(T) are the decay constants at 15ºC and T ºC and Q_{10} is the Arrhenius temperature coefficient, set to 2.2 for C, 2.0 for N and 1.5 for P.

Results

Environmental conditions

During the sampling period wind direction was predominantly equatorward with intensities of 6 to 13 m s^{-1}, which is characteristic of the trade wind regime normally found in the study area (Table 1). Poleward winds were only found at sta. 3 during the early dry season (Table 1). Sta. 1 and 2 could potentially have been impacted by upwelling events that occur mostly from October to March (summer), when the south-easterly trade winds relax and monsoon winds are active. However, a recent study (Benthuysen et al. 2016), which characterized

upwelling events in the GBR over the period 2010 to 2015, did not detect any events within the weeks of our sampling times and impact on our results therefore seems unlikely.

The observed Secchi-disk depth varied between 1 and 20 m, with highest levels at the most offshore station (sta. 2). TSS concentrations were highest (up to 5.86 ± 0.74 mg L^{-1}) at the nearshore station (sta. 3) and lowest at the offshore station (sta. 2) (Table 1). Suspended matter concentrations increased at all stations with wind speed and the levels were inversely related to Secchi-disk depth ($R^2 = 0.49$, $p < 0.01$).

During the late dry season, surface salinities and temperatures were equal (T-Student, $p > 0.05$) at the three locations with levels of around 35.5 and 25ºC, respectively. Alongside, Chl *a*, DIN and DIP showed fairly similar levels at the three sites (T-Student, $p > 0.05$). (Table 1). In the wet season surface salinities were also around 35.5, but temperatures and Chl *a* values were at the highest, around 28ºC and up to 0.84 ± 0.04 µg L^{-1}, respectively. Lowest DIN concentrations were measured during this period, while DIP was maintained at a similar level to those found during the other seasons (Table 1). Finally, during the early dry season salinity levels were again around 35.5, temperatures had decreased to 23-24ºC, comparable to the late dry season, and Chl *a* concentrations ranged from 0.29 ± 0.05 to 0.54 ± 0.03 µg L^{-1}. The DIN concentrations were at levels comparable to the late dry season, while DIP showed similar concentrations to those measured during the two other seasons (Table 1). Field concentrations of POC varied between 6.5 ± 0.2 and 16.2 ± 0.9 µmol L^{-1}, while PN and PP ranged from 0.84 ± 0.22 to 2.43 ± 0.25 µmol L^{-1} and from 0.06 ± 0.01 to 0.19 ± 0.03 µmol L^{-1}, respectively (Table 1). The field POC, PN and PP concentrations were all related (R^2 varying between 0.61 and 0.91, $p < 0.01$) with the TSS levels. Since TSS concentrations in the inshore GBR lagoon is dominated by resuspended sediment, it suggests that the changes we measure in field POM concentrations were related to resuspension events (Lambrechts et al. 2010).

313

314 **Particulate and dissolved organic matter concentrations and bioavailability**

315 Initial POC concentrations in the degradation experiments varied between 15 ± 3 and 39 ± 3
316 μmol L^{-1}, while PN and PP ranged from 2.6 ± 1.4 to 5.6 ± 0.3 μmol L^{-1} and from 0.13 ± 0.04
317 to 0.38 ± 0.06 μmol L^{-1}, respectively (Table 2). The initial DOC concentrations in the DOM
318 degradation experiments varied from 57 ± 1 to 84 ± 2 μmol L^{-1}, DON from 4.7 ± 0.3 to 6.2 ±
319 1.0 μmol L^{-1}, and DOP from 0.16 ± 0.05 to 0.28 ± 0.04 μmol L^{-1} (Table 2). These DOM
320 levels were comparable to concentrations normally found in the GBR lagoon (Furnas et al.
321 2011). There was no significant difference in the initial inorganic nutrient and DOM
322 concentrations between the DOM and POM experiments (data not shown), suggesting that
323 our pre-concentration of the suspended solids did not cause any major lysis of plankton cells.
324 Organic matter bioavailability and degradation rates are difficult to measure directly in the
325 field. In our incubations we are unable to account for all processes involved in in-situ OM
326 degradation and the approach is therefore simplistic. The experiments are closed to new
327 production and therefore force the microbial community to use the OM produced in-situ prior
328 to the experiments. In this study we defined the recalcitrant pool as the concentration in the
329 samples taken after 50 days of incubation, but we acknowledge that a true estimate of the
330 recalcitrant pool will probably never be obtained in these type of experiments.
331 After 50 days of incubation bioavailable POM ranged between 7 ± 5 and 29 ± 6 μmol L^{-1}
332 for C, 2.0 ± 0.5 and 4.9 ± 1.2 μmol L^{-1} for N, and 0.12 ± 0.05 and 0.35 ± 0.16 μmol L^{-1} for P
333 (Table 2; Figure 2). This corresponded to average bioavailable fractions of 58 ± 8 % (average
334 ± SE) for POC, 75 ± 6 % for PN, and 90 ± 3 % for PP (Table 2; Figure 2). Within the initial 4
335 days, a conversion of the particulate pool into new DOM was measured, resulting in a peak
336 DOM concentration at day 4 (Figure 4). After that, decreasing concentrations were found

337 until day 50, reaching similar endpoint DOM values as those found in the DOM experiment
338 (Figure 4).
339 In the DOM degradation experiments the bioavailable DOC (BDOC) varied between 6 ± 5
340 and 21 ± 4 μmol L^{-1} corresponding to 16 ± 5 % of DOC (average ± SE), bioavailable DON
341 (BDON) ranged between 1.5 ± 0.5 and 2.5 ± 1.3 μmol L^{-1} representing 32 ± 4 % of the DON
342 and bioavailable DOP (BDOP) reached values between 0.09 ± 0.08 and 0.21 ± 0.07 μmol L^{-1}
343 corresponding to 68 ± 8 % of DOP (Table 2; Figure 3). BDOM significantly correlated with
344 inorganic nutrients and Chl *a* (Table 3), indicating that the differences in DOM
345 bioavailability were related to the variations in plankton biomass and activity. The
346 recalcitrant DOM concentrations were not significantly different in the three experiments,
347 except at sta. 2 during the late dry season that showed very low values (RDOC: 51 ± 1 μmol
348 L^{-1}; RDON: 3.2 ± 0.3 μmol L^{-1}; RDOP: 0.08 ± 0.04 μmol L^{-1}).
349
350 **Contribution of organic matter to the bioavailable nutrient pools**
351 The contribution of DON and DOP to the regeneration of inorganic nutrients was calculated
352 as the slope of the BDON vs. DIN and BDOP vs. DIP linear regressions showing that 19 ±
353 5 % of the DIN and 54 ± 12% of the DIP originated from the degradation of the bioavailable
354 fractions of DON and DOP, respectively (Eq. 1 and 2; Table 4). Our work also showed that
355 on average POM contained 35 ± 10 % and 25 ± 8%, and the DOM fraction contained 60 ± 10
356 % and 50 ± 10 % of the total bioavailable N and P in this system (Figure 5).
357 Positive linear relationships were found between the bioavailable and total pools for both
358 POM and DOM (Eq. 3 to 8; Table 4), with regression slopes not significantly different from
359 1. This suggests that when bioavailable concentrations increased by 1 μmol L^{-1}, the total pool
360 increased by 1 μmol L^{-1}, demonstrating that the variations in concentrations were due to
361 bioavailable components. The origin intercepts of these regressions indicate the average

362 recalcitrant POM and DOM levels (Eq. 3 to 8; Table 4). The recalcitrant POM concentrations
363 cannot directly be compared with in-situ levels as we applied a pre-concentration step. For
364 the DOM pool average recalcitrant concentrations were 55 ± 5 μmol L^{-1} for DOC, 3.4 ± 0.8
365 μmol L^{-1} for DON, and 0.07 ± 0.03 μmol L^{-1} for DOP (Table 4).
366
367 **Organic matter stoichiometry**
368 The average C: N: P stoichiometry for the POM pool was 115 (± 9): 20 (± 4): 1, while the
369 bioavailable POM pool had a lower ratio of 75 (± 8): 17 (± 1): 1 (Figure 6). The average
370 C:N:P stoichiometry of the DOM pool was 332 (± 27) :25 (± 2):1 and BDOM was 83 (±
371 37):12 (± 2):1 (Figure 6). The C:N:P stoichiometry of the recalcitrant POM (552 (± 133): 56
372 (± 22):1) and DOM (936 (± 310): 58 (± 21):1) were not different among them and showed
373 that they were particularly N- and P- depleted compared with the total and bioavailable
374 fractions.
375
376 **Organic matter degradation rates**
377 In order to model the time course of POM and DOM degradation during the incubation
378 experiments we used an exponential model that considers only two pools (Eq. 1 and 2):
379 bioavailable and recalcitrant. Average POM degradation rates were 0.25 ± 0.05 d^{-1} (average ±
380 SE) for POC (k_{POC}), 0.29 ± 0.04 d^{-1} for PN (k_{PN}) and 0.34 ± 0.05 d^{-1} for PP (k_{PP}) (Table 5).
381 The degradation rates for the bioavailable DOM pool were lower than for the bioavailable
382 POM pool with average first-order rate constants of 0.13 ± 0.05 d^{-1} for DOC (k_{DOC}), 0.16 ±
383 0.07 d^{-1} for DON (k_{DON}) and 0.24 ± 0.08 d^{-1} for DOP (k_{DOP}) (Table 5). Positive correlations
384 were also observed between C, N and P degradation rates either for POM (Eq. 9 to 11; Table
385 4) or DOM (Eq. 12 to 14; Table 4), with the regression slopes, indicating that N and P
386 containing compounds (e.g. amino acids) are degraded faster than N and P poor compounds

(e.g. long chain fatty acids) leading to the C-rich recalcitrant POM and DOM pools referred above. Both the POM and DOM degradation rates were positively correlated with the size of the bioavailable pools (Eq. 15 to 17 and 18 to 20 of Table 4), demonstrating that higher bioavailable concentrations would lead to faster degradation rates. As our POM degradation rates were calculated on concentrated samples they are not directly comparable with in-situ rates. We therefore only calculated half-life time ($\ln 2/k_M$) for the BDOM pool that were 4.8 ± 1.6 d for DOC, 3.7 ± 1.3 d for DON and 2.7 ± 0.7 d for DOP. To compare our DOM degradation rates with other values in the literature, we estimated the first order degradation rate constants at a standard temperature of 15ºC, resulting in average k_{DOC} of 0.05 ± 0.02 d^{-1}, k_{DON} of 0.07 ± 0.02 d^{-1} and k_{DOP} of 0.15 ± 0.04 d^{-1}, which translate into half-life times of 14.7 ± 4.9 d for DOC, 10.1 ± 3.4 d for DON and 4.7 ± 1.3 d for DOP.

Discussion

Organic matter (OM) degradation has a major impact on the distribution of carbon, nitrogen and phosphorus in the oceans (Hansell et al. 2009; Hedges 2002; Lønborg and Álvarez-Salgado 2012). At the global coastal ocean scale, about 50% of the net primary production is supported by pelagic mineralization and an additional 25% by benthic mineralization of biogenic organic matter (Wollast 1998). Determining the reactivity of OM is therefore critical for our understanding of the ocean carbon, nitrogen and phosphorus cycles. However, few data are available on the amount of labile compounds and the rate of degradation of both POM and DOM in tropical coastal waters.

Organic matter bioavailability

The particulate matter collected in our study was a mixture of inorganic particles, living OM and detritus. Because of the shallow nature of the GBR lagoon (especially at sta. 1 and 3) the

412 water is often turbid (classified as ‘case 2’ waters) and it has been demonstrated that POM
413 recovered is mainly sediment derived with only a part being produced daily by the plankton
414 community (Furnas et al. 2011; Furnas et al. 2005). At all our stations POM and TSS levels
415 were correlated illustrating the importance of suspended sediment OM in our POM
416 incubation experiments. Sediment OM in the GBR has been shown to be readily degraded
417 with only around 1% of the combined river and marine OM being preserved in the sediments
418 (Alongi et al. 2007; Brunskill et al. 2002). In accordance with these and studies conducted in
419 other coastal systems we found that a large part of the C, N and P in the POM pool was
420 bioavailable over the 50 days incubation period (Burkhardt et al. 2014; Fujii et al. 2002;
421 Garber 1984; Seiki et al. 1991; Wetz et al. 2008). This high bioavailability fits well with the
422 major contribution of carbohydrates and proteins found in the POM pool of the Great Barrier
423 Reef (Lønborg et al. 2017). But it should also be kept in mind that not all PN and PP in our
424 experiments was organic as parts likely were particle –bound inorganic nitrogen and
425 phosphorus (Eyre 1994; Sanudo-Wilhelmy et al. 2004). Since we did not quantify this
426 contribution, our PN and PP bioavailability are likely overestimated.
427 Particles and aggregates are known to be hot spots of microbial enzymatic activity
428 transforming POM into DOM often at rates faster than can be used, thereby releasing DOM
429 that can be utilized by free-living microbes (Kahler and Koeve 2001; Smith et al. 1992). This
430 enzymatic activity conversion has previously been shown and was also observed in our study
431 (Figure 4). This degradation pattern, as also found in this study, follows three main phases
432 (1) a “leaching phase” resulting in a decrease in particles and increase in DOM and inorganic
433 nutrient concentrations, (2) a “degradation phase” where both POM and DOM are partly
434 converted into microbial biomass and partly respired to CO_2 and inorganic nutrients, and
435 finally (3) the “recalcitrant phase” where no further degradation is taking place (e.g. Fukami
436 et al. 1985; Harrison and Mann 1975; Valiela et al. 1984). Previous studies have found that

around 30% of phytoplankton-derived OM is bioavailable (Buchan et al. 2014), but in our study we found that the recalcitrant DOM concentrations in the POM and DOM were not different, suggesting that the DOM produced during the "leaching" and degradation phases" was bioavailable within the 50 days incubation period.

Our measurements show that DOM had bioavailabilities comparable to the average values reported for coastal waters worldwide (DOC: 22 ± 12%; DON: 35 ± 13%; DOP: 70 ± 18%) (Lønborg and Álvarez-Salgado 2012). These were consistently lower than for the POM pool, suggesting a more recalcitrant nature of the DOM pool. This finding is in accordance with the size-reactivity continuum model, which suggests that as OM is degraded it become less bio-reactive and smaller in size (Amon and Benner 1996; Benner and Amon 2015). This difference in POM and DOM bioavailability could be linked with the fact that a larger proportion of particulate forms are found in known biochemical classes (e.g. carbohydrates, proteins, lipids, nucleic acids) than in the dissolved fraction, suggesting that in general DOM is more reworked and recalcitrant (Benner 2002; Benner and Kaiser 2003; Hama et al. 2004; Wakeham et al. 1997).

The average recalcitrant DOM concentrations measured in our study (RDOC: 51 ± 1 μmol L^{-1}; RDON: 3.2 ± 0.3 μmol L^{-1}; RDOP: 0.08 ± 0.04 μmol L^{-1}), were lower than average values reported for coastal waters worldwide (RDOC: 255 ± 295 μmol L^{-1}; RDON: 10.1 ± 7.3 μmol L^{-1}; RDOP: 0.12 ± 0.07 μmol L^{-1}(Lønborg and Álvarez-Salgado 2012)), but only slightly higher than found in deep ocean water: 35–45 μmol L^{-1} for DOC (Hansell et al. 2009), 3.6 ± 0.8 μmol L^{-1} for DON (Sipler and Bronk 2015) and <0.05 μmol L^{-1} for DOP (Karl and Björkman 2015). Recalcitrant DOM in coastal waters have previously been shown to be mainly of terrestrial origin (Lønborg and Álvarez-Salgado 2012), but as our sites had relative high salinities (> 35) the ocean influence is predominant and thus, we obtained recalcitrant DOM levels closer to open ocean concentrations.

462 The % POM and DOM bioavailability was variable between experiments, but there was
463 no clear seasonal or location pattern. Organic matter bioavailability has traditionally been
464 linked with its biochemical composition, but more recently it has been shown that molecular
465 structure does not alone control the bioavailability, but depending on environmental factors
466 too (Raymond and Spencer 2015). These factors include changing temperature and nutrient
467 regimes, varying terrestrial inputs, biological production of recalcitrant compounds, sun-light,
468 changing bacterial community and chemical composition, the presence of lithogenic particles
469 and the effect of priming (e.g. Del-Giorgio and Davies 2003; Kawasaki and Benner 2006;
470 Keil and Mayer 2014; Ward et al. 2016). Some studies suggest that the microbial degradation
471 of OM could be limited by inorganic nutrients (Thingstad et al. 1999), which are particularly
472 low in the Great Barrier Reef (<0.25 μmol L^{-1} of DIN, <0.10 μmol L^{-1} of DIP). We found that
473 the inorganic nutrient concentrations increased over the incubation period, suggesting that
474 over time the microbial degradation was not limited by the nutrient availability. Another
475 factor that also likely influences the bioavailability is the contribution of terrestrial and
476 marine derived matter, with terrestrial material being less bioavailable than marine derived
477 material (Bauer et al. 2013). In our study, as suggested by the salinities (> 35), the influence
478 of terrestrial derived OM was minor and changes in the bioavailability is therefore more
479 likely related to marine processes. Aquatic microbes have been shown to produce recalcitrant
480 OM when degrading bioavailable compounds (Kawasaki and Benner 2006; Lønborg et al.
481 2009a; Ogawa et al. 2001). These processes did most likely also take place in our
482 experiments but we are unfortunately not able to determine the impact on our results. Sun-
483 light related processes have been shown to both enhance and decrease OM bioavailability,
484 with the impact most likely depending on the microbial community involved and the OM
485 chemical composition (Mayer et al. 2009; Tranvik and Bertilsson 2001). As we conducted
486 our experiments in the dark we cannot assess how sunlight impacts the OM bioavailability.

The microbial community composition varies spatially, seasonally and during incubation experiments (Massana et al. 2001; Teira et al. 2009). Changes in the microbial community most likely occurred during our experiments, but as we did not quantify these changes we are not able to assess how this impacted the bioavailability. There is also growing evidence that some minerals can enhance and others protect OM from microbial degradation (Keil and Mayer 2014). As there were variable levels of inorganic particles present in our field samples (TSS levels reported in Table 1) these were added to our POM experiments. We cannot exclude the possibility that these processes impacted our results, but as we did not find any clear relationship between initial TSS concentrations and particles bioavailability the overall influence is likely minor. The priming effect refers to the observation that addition of labile OM can modify or trigger degradation of previously recalcitrant OM (Blagodatskaya and Kuzyakov 2008). Few studies have investigated these processes in marine waters mostly demonstrating contrasting outcomes, with some suggesting no or negative priming (decreased bioavailability) and others finding positive priming (increased bioavailability) effects (e.g. Carlson et al. 2002; Carlson et al. 2004; Cherrier et al. 1999; Gontikaki et al. 2013). Our POM experiments where we added highly labile POM to the DOM pool can be used as an initial test of whether priming is influencing DOM degradation in the GBR. As we did not find any enhanced DOM degradation in those experiments there is no indication of priming. But as our experiments were conducted under lab-based conditions, more complex sets of conditions (e.g. changed microbial community and array of labile substrates) are needed to be tested before it can be concluded if priming is important for the OM cycling in the GBR (Bianchi 2011; Ward et al. 2016).

For our bioavailability estimates it should be noted that these are based on laboratory experiments, which ignores that in nature the POM and DOM pools would be mixed with other water masses and OM from different sources. Furthermore, in nature the pools are also

512 exposed to other water-column processes such as turbulence, photochemical reactions,
513 sedimentation and resuspension that might influence their bioavailability. Despite this
514 limitation our data shows that the POM and DOM pools are partially bioavailable on a time
515 scale of days to weeks.

516 In order to understand the nutrient dynamics in coastal waters it is necessary to account for
517 both inorganic and the bioavailable part of organic nutrients. We show that in oligotrophic
518 tropical coastal waters such as the GBR where the inorganic nutrient concentrations are close
519 to the detection limit levels of the standard methods, on average 95 ± 2 % of the bioavailable
520 nitrogen and 75 ± 7 % of the bioavailable phosphorus are contained in the organic fraction.
521 Our study suggests that in the GBR, future work should focus on measuring the total nutrient
522 bioavailability and not only, as previously, focus on inorganic nutrient concentrations.
523

524 **Particulate versus dissolved organic matter stoichiometry**

525 The stoichiometry of OM is a signature of production and degradation pathways. While the
526 C:N:P ratios of POM and plankton biomass are relatively well constrained at a mean value of
527 106:16:1, i.e. the Redfield ratio (Anderson 1995; Redfield et al. 1963); the elemental ratios of
528 DOM during both production and degradation processes is less well understood (Conan et al.
529 2007; Hopkinson and Vallino 2005).

530 Previous studies in oligotrophic environments have shown that the N:P of particulate
531 matter tended to exceed the Redfield ratio of 16 (e.g. Hebel and Karl 2001). In contrast, in
532 the GBR the C:N:P ratios in suspended particulate matter are very close to Redfield ratio
533 (Average: 115:14:1, $n = 838$), suggesting a major contribution of plankton sourced material
534 and a minor influence of continental OM (e.g. mangroves, salt marshes, seagrasses) which
535 have higher C:N:P ratios (Vitousek et al. 1988). On the other hand, the DOM pool in the

536 GBR has average ratios much higher than Redfield (302:27:1, *n* = 1011). Both the POM and
537 DOM ratios show only minor temporally or cross-shelf variations (Furnas et al. 2005).
538 The stoichiometry of both the bioavailable POM and DOM pools is compatible with the
539 product of synthesis and early degradation of marine phytoplankton (Anderson 1995; Garber
540 1984; Redfield et al. 1963). Therefore, the DOM is degraded with a C: N : P ratio
541 substantially lower than for the bulk pool. In coastal waters the BDOM stoichiometry has
542 been shown to vary between 483: 38: 1 and 57:13:1, with an overall average of 197: 25 :1
543 (Lønborg and Álvarez-Salgado 2012), which is comparable to ratios found in the open ocean
544 (300: 22:1, Benner 2002 ; 199: 20: 1, Hopkinson and Vallino 2005 ; 317:39:1, Letscher and
545 Moore 2015). Our estimate (83 (± 37):12 (± 2):1) is lower than these average values, which
546 could be linked with difference in the plankton release of C-rich labile compounds (e.g.
547 mono- and polysaccharides) (Fajon et al. 1999), chemical composition, and/or changes in the
548 production and degradation pathways between systems (Torres-Valdes et al. 2009). The
549 stoichiometry of both the bioavailable POM and DOM concurs with both the fractionation
550 during OM degradation, and our finding of the C, N and P containing compounds being more
551 bioavailable than the C and N containing compounds that are in turn more bioavailable than
552 C containing compounds. This therefore explains the increasing C: N and C: P ratios found
553 with depth for exported OM in the deep ocean and in microbial degradation experiments
554 (Berggren et al. 2015; Boyd and Trull 2007; Hopkinson and Vallino 2005; Lønborg and
555 Álvarez-Salgado 2012 and references therein).
556 Conversely, the C:N:P stoichiometry of the recalcitrant POM and DOM pools were
557 characterized by being extremely N- and P- depleted compared to the bioavailable fraction.
558 It is remarkable that the C:N:P ratios found for both the recalcitrant POM (552 (± 133): 56 (±
559 22):1) and DOM pools (936 (± 310): 58 (± 21):1) were less N- and P- depleted than values
560 reported for open (3511: 202: 1), coastal (2835: 159: 1) and terrestrial recalcitrant OM

561 (3495: 118: 1) (Hopkinson and Vallino 2005; Lønborg and Álvarez-Salgado 2012; Meybeck
562 1982). This relative N and P enrichment could be due to that our incubation period was short
563 (50 days) and therefore not all semi-labile OM was consumed. In any case, recalcitrant DOM
564 can be then considered as the DOM that was not utilized by heterotrophic bacteria during the
565 incubation independently of what was the cause behind: recalcitrant chemical structure,
566 environmental conditions, extreme dilution of individual molecules, etc. (Dittmar 2015; Goto
567 et al. 2017). Although recalcitrant DOM can be produced by abiotic processes, recent
568 incubation experiments have also demonstrated that the molecular and structural properties of
569 microbial derived DOM are consistent with those of the recalcitrant molecules in the ocean
570 (Lechtenfeld et al. 2015; Osterholz et al. 2015). Concerning the molecular composition of
571 recalcitrant DOM, carboxyl-rich aliphatic materials, CRAM (Hertkorn et al. 2006),
572 polyaromatic compounds (Dittmar and Paeng 2009) and, to a minor extend, humic-like
573 materials (Catala et al. 2015; Yamashita and Tanoue 2008) have been already identified. All
574 of them are N and P depleted compounds.
575
576
577 **Organic matter degradation rates**
578 Biologically produced OM has different reactivates, with degradation being a multi-step
579 process, as the pool contains a spectrum of reactive compounds, each with its own rate of
580 degradation (e.g. Vahatalo et al. 2010). However, in most studies degradation has been
581 modelled assuming exponential decay and one bioavailable pool decaying with a first-order
582 rate constant.
583 The rates of OM degradation have previously been shown to vary depending on the
584 microbial community composition, redox state, environmental conditions and
585 sorption/desorption of organic molecules to particles (Keil and Mayer 2014). The rates we

586 determined in this study are not directly comparable with in-situ rates as we e.g. diluted the
587 microbial community, applied a pre-concentration step in the POM experiment and ignored
588 the influence of various processes including turbulence and photochemical reactions.
589 In spite of these limitations, our data demonstrate that natural derived POM and DOM can
590 be degraded on timescales of days (e.g. Bendtsen et al. 2015; Burkhardt et al. 2014; Seiki et
591 al. 1991; Wetz et al. 2008) and that the microbial degradation slowed down over time
592 reaching a stable level at the end of the experiments. Both the POM and DOM degradation
593 rates were positively correlated with the bioavailable pool (Table 2), demonstrating that
594 higher bioavailable concentrations would lead to faster degradation, as also observed
595 previously (e.g. Hopkinson et al. 1997; Lønborg et al. 2009b). Positive correlation was
596 observed between C, N and P degradation rates for the POM and DOM pools. The
597 corresponding linear regression slopes, indicated that the POC and DOC pools were degraded
598 at a rate equivalent to 73 ± 26 and 55 ± 6% (slope ± SE) of PP and DOP, respectively (Table
599 4). While the PN and DON pools were degraded at a rate equivalent to 85 ± 27% and 67 ±
600 15% of PP and DOP, respectively (Table 4). This is in agreement with the bioavailability and
601 the C:N:P stoichiometry estimates, demonstrating that C, N and P-containing molecules are
602 more reactive than C and N- containing molecules, which in turn are more labile than C-
603 containing molecules.
604 The degradation of POM has been studied extensively in open ocean waters with
605 degradation rate constants estimated in laboratory and field settings using both natural and
606 specific OM sources (e.g. phytoplankton cells, faecal pellets) (e.g. Goutx et al. 2007; Harvey
607 and Macko 1997; Harvey et al. 1995; Panagiotopoulos et al. 2002; Sempéré et al. 2000).
608 Previous studies have shown that the POC exponential degradation constants vary widely
609 (approx. range 0.001– 0.72 d^{-1}) both between studies and with source material, with most
610 rates reported for POC and fewer for PN and PP (Goutx et al. 2007; Harvey et al. 1995;

611 Panagiotopoulos et al. 2002). Our average POM degradation rate (0.25 ± 0.05 d^{-1} for POC;
612 0.29 ± 0.04 d^{-1} for PN and 0.34 ± 0.05 d^{-1} for PP at 22-24°C) were similar between stations
613 and seasons. The POC rates were 1/2 to 1/3 lower than rates obtained at similar temperatures
614 for freshly produced phytoplankton POC (~ 19°C, Harvey et al. 1995 ; 27°C, Hama et al.
615 2004), but comparable to rates found for the degradation of amino acids (0.13 ± 0.03 d^{-1}),
616 lipids (0.24 ± 0.11 d^{-1}) and natural organic material (range from 0.01 to 0.50 d^{-1}) collected in
617 sediment traps (Belcher et al. 2016; Boyd et al. 2015; Goutx et al. 2007; Mcdonnell et al.
618 2015).

619 Degradation rates for the DOM pool obtained from incubation experiments vary widely
620 with DOC rates (normalized to 15ºC) ranging between 0.001 d^{-1} for samples collected in
621 Florida Bay (Boyer et al. 2006) and up to as high as 0.97 d^{-1} for plankton derived material
622 collected off the coast of Oregon (Wetz et al. 2008). In our experiments the DOM
623 degradation rates (0.13 ± 0.05 d^{-1} for DOC, 0.16 ± 0.07 d^{-1} for DON and 0.24 ± 0.08 d^{-1} for
624 DOP) were similar to average values reported for coastal waters (Lønborg and Álvarez-
625 Salgado 2012) and showed generally similar rates between stations and seasons. As both the
626 POM and DOM rates did not shown any seasonal or spatial difference it points to similarities
627 within each pool in the biochemical composition and the factors controlling the rates. This
628 lack of variability is in line with previous studies in the GBR showing only minor seasonal
629 and spatial differences in plankton productivity and metabolism, and in the contribution of
630 carbohydrates and proteins to the POM and DOM pools (Furnas and Mitchell 1987; Lønborg
631 et al. 2017; Mckinnon et al. 2013).

632 In the warm oligotrophic waters of the GBR the phytoplankton community shows rapid
633 growth and relative high productivity, which is thought to be fuelled by a steady supply of
634 nutrients from OM degradation (Furnas et al. 2005). Despite the importance of these
635 processes in sustaining productivity few studies have investigating the element cycling in the

636 GBR. One such study investigated the ammonium regeneration rates using a stable isotope
637 approach at Davies Reef, south of our study area, measuring an average production rate of
638 0.10 ± 0.01 μmol N L^{-1} d^{-1} (ranging from undetectable up to 0.27 μmol N L^{-1} d^{-1}; (Hopkinson
639 et al. 1987). Another study estimated that on average a daily supply of 0.24 μmol N L^{-1} and
640 0.015 μmol P L^{-1} was needed to sustain the plankton primary productivity (Furnas et al.
641 2005). If we assume that the bioavailable compounds are replenished on a daily scale and all
642 POM is available for degradation, we can use our degradation rates to calculate a likely upper
643 limit for the nitrogen and phosphorus supplied by POM and DOM degradation. This
644 calculation shows that the POM pool could provide on average 0.35 ± 0.17 μmol N L^{-1} d^{-1}
645 and 0.03 ± 0.02 μmol P L^{-1} d^{-1}, while the DOM pool could supply 0.33 ± 0.15 μmol N L^{-1} d^{-1}
646 and 0.03 ± 0.11 μmol P L^{-1} d^{-1}. These values are, individually and combined, larger than the
647 daily supply needed, suggesting that the OM pool contains sufficient labile material to fuel
648 the plankton primary productivity in the GBR.
649 From a biogeochemical perspective, it is important to compare our degradation rates with
650 the residence times to determine if the bioavailable OM is degraded before being transported
651 into the Coral Sea through physical processes (e.g. cross-shelf mixing or advection).
652 Different approaches (e.g. hydrodynamic models and satellite tracked drifters) have been
653 used to calculate the residence time in the GBR providing very diverse estimates (varying
654 between 7 and 430 days; Choukroun et al. 2010; Luick et al. 2007). In this study we
655 therefore chose to use a conservative estimate of the residence time (2 weeks; Choukroun et
656 al. 2010) to compare with our degradation rates and half-life times. From these estimates it is
657 clear that most of the bioavailable POM and DOM would be consumed (BPOM > 96%;
658 BDOM > 83%) within the system before reaching the outer shelf. The fractionation we
659 measured also suggests that the material that would be exported to the sediment (POM),
660 and/or to the Coral Sea (DOM), will be carbon rich, which might influence the N/P limitation

661 of the receiving systems. This finding is in agreement with a previous attempt to balance the
662 GBR carbon budget using a radioisotope approach, which suggested a near balance between
663 production and respiration and following a small export of C, N and P from the GBR lagoon
664 to the Coral Sea (Brunskill et al. 2010).
665
666 ***Conclusions***
667 In this study, we demonstrate that in the coastal waters of the GBR: 1) the bioavailability
668 of the POM pool is much larger than for the DOM pool; 2) on average 95 ± 2 % of the
669 bioavailable nitrogen and 75 ± 7 % of the bioavailable phosphorus are contained in the
670 organic fraction; 3) the bioavailable POM pool has a stoichiometry demonstrating a
671 preferential degradation of N-rich materials, i.e. proteins, compared to the average Redfield
672 ratio, while the bioavailable DOM is enriched in N and P compared with the whole pool; 4)
673 the degradation rates suggest that the organic fraction contains sufficient labile material to
674 sustain the GBR plankton primary productivity in the GBR; and 5) most of the bioavailable
675 POM and DOM is consumed within the GBR lagoon and thus there is only a small export of
676 C, N and P to the Coral Sea.
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1027

1028 **Acknowledgments**

1029 Financial support for this study was provided by the Australian Institute of Marine Science.

1030 We thank the crew of the R.V. *Cape Ferguson* for help at sea. The help of the Cruise leader

1031 (Irena Zagorskis) and other participants (Paul Costello and Johnstone Davidson) in obtaining

1032 the field data is also acknowledged. The field data included in the manuscript was obtained

1033 with support from the Great Barrier Reef Marine Park Authority, through funding from the

1034 Australian Government Reef Program and from the Australian Institute of Marine Science.

1035 X.A.A.S was support by the CSIC project FOMEM (grant No PIE 201030E130).

1036 **Figure legends**

1037 **Fig. 1.** Map showing the three sampling stations (●) that were sampled during three cruises
1038 aboard R/V *Cape Ferguson* in the period September 2014 to June 2015. The offshore
1039 arrows show the East Australian Current (EAC) which flows poleward and enters onto the
1040 shelf and outer lagoon by passages between reefs. The arrow close to shore indicates the
1041 coastal current which is predominantly equatorward. **Fig. 2.** Time course of a), b), c)
1042 particulate organic carbon (POC), d), e), f) nitrogen (PN) and g), h), i) phosphorus (PP)
1043 during the microbial incubation experiments from the three different stations. Figures a),
1044 d) and g) represent the experimental data obtained for sta. 1, b), e), h) for sta. 2 and c), f),
1045 i) for sta. 3 during the late dry (●), wet (●) and early dry (○) seasons. Error bars represent
1046 standard errors.

1047 **Fig. 3.** Time course of a), b), c) dissolved organic carbon (DOC), d), e), f) nitrogen (DON)
1048 and g), h), i) phosphorus (DOP) during the microbial incubation experiments from the
1049 three different stations. Figures a), d) and g) represent the experimental data obtained for
1050 sta. 1, b), e), h) for sta. 2 and c), f), i) for sta. 3 during the late dry (●), wet (●) and early
1051 dry (○) seasons.. Error bars represent standard errors.

1052 **Fig. 4.** Example of the time evolution, of a) total (TOC) particulate (POC) and dissolved
1053 organic carbon (DOC), b) total nitrogen (TN), particulate organic nitrogen (PON),
1054 dissolved inorganic (DIN) and organic (DON) nitrogen; c) total phosphorus (TP),
1055 particulate organic phosphorus (POP) dissolved inorganic (DIP) and organic (DOP)
1056 phosphorus in the experiment conducted at sta. 3 in the late dry season. Error bars
1057 represent standard errors.

1058 **Fig. 5.** Average distribution of bioavailable a) phosphorus and b) nitrogen between dissolved
1059 inorganic nutrients, particulate and dissolved organic matter from the three different

1060 stations in Late dry (September 2014), Wet (February 2015) and Early dry seasons (June
1061 2015). Error bars represent standard errors.
1062 **Fig. 6.** X–Y plots of (a) B-PN versus B-POC (●), BDON with BDOC (○), (b) B-PP versus B-
1063 POC (●), BDOP with BDOC (○) and (c) B-PP versus B-PN (●), BDOP with BDON (○).
1064 Solid and dashed lines represent the corresponding regression and error bars are standard
1065 errors. R^2 = coefficient of determination, p = significant level.
1066

1067 **Table 1.** Meteorological conditions, and physical, chemical and biological properties of the surface (5 m) water samples at the time of
1068 collection. Wind direction (Wind dir.) and speed are shown together with average values for salinity (Sal.), temperature (Temp.), Secchi disk
1069 depth, total suspended solids (TSS), chlorophyll *a* (Chl *a*), dissolved inorganic nitrogen (DIN= NH_4^++ NO_3^-/NO_2^-) and phosphorus (DIP),
1070 particulate organic carbon (POC), nitrogen (PN) and phosphorus (PP) are shown. Standard deviations are shown for Chl *a*, nutrient and
1071 particulate organic matter data.

Stn.	Season	Wind dir.	Wind speed m s^{-1}	Sal.	Temp. ºC	Secchi depth m	TSS mg l^{-1}	Chl. *a* µg l^{-1}	DIN µmol l^{-1}	DIP µmol l^{-1}	POC µmol l^{-1}	PN µmol l^{-1}
1	Late dry	E	7	35.4	24.7	10	0.48 ± 0.12	0.16 ± 0.02	0.17 ± 0.05	0.08 ± 0.02	6.7 ± 0.1	0.84 ± 0.22
	Wet	SE	7	35.4	28.3	5	1.10 ± 0.15	0.70 ± 0.05	0.04 ± 0.04	0.04 ± 0.02	7.9 ± 0.6	1.25 ± 0.05
	Early dry	SSW	7	35.5	24.3	6	0.82 ± 0.18	0.29 ± 0.05	0.14 ± 0.05	0.07 ± 0.01	6.5 ± 0.2	0.93 ± 0.13
2	Late dry	E	6	35.4	24.7	20	0.11 ± 0.07	0.08 ± 0.02	0.21 ± 0.07	0.06 ± 0.01	7.7 ± 0.6	1.42 ± 0.08
	Wet	SE	13	35.4	28.4	8	0.46 ± 0.10	0.43 ± 0.06	0.20 ± 0.03	0.09 ± 0.02	7.7 ± 0.4	1.24 ± 0.12
	Early dry	ESE	8	35.5	24.2	5	1.12 ± 0.96	0.39 ± 0.08	0.13 ± 0.03	0.06 ± 0.02	8.1 ± 1.0	1.43 ± 0.09
3	Late dry	ENE	6	35.7	24.7	7	1.69 ± 0.79	0.26 ± 0.13	0.23 ± 0.05	0.10 ± 0.02	11.5 ± 3.7	1.44 ± 0.43
	Wet	E	12	35.7	28.2	1	5.86 ± 0.74	0.84 ± 0.04	0.11 ± 0.01	0.10 ± 0.01	16.2 ± 0.9	2.43 ± 0.25
	Early dry	ESE	9	35.7	23.3	3	2.49 ± 0.20	0.54 ± 0.03	0.18 ± 0.03	0.07 ± 0.02	11.9 ± 4.9	1.69 ± 0.09

1072

Table 2. Initial (POC, PN, PP, DOC, DON, DOP), recalcitrant (R-POC, R-PN, R-PP, R-DOC, R-DON, R-DOP), and bioavailable (B-POC, B-PN, B-PP, B-DOC, B-DON, B-DOP) concentrations of a) particulate (POM) and b) dissolved organic matter (DOM) determined during the experiments. Values are averages ± standard error.

a)

Station	Season	POC μmol L^{-1}	B-POC μmol L^{-1}	R-POC μmol L^{-1}	PN μmol L^{-1}	B-PN μmol L^{-1}	R-PN μmol L^{-1}	PP μmol L^{-1}	B-PP μmol L^{-1}	R-PP μmol L^{-1}
1	Late dry	24 ± 8	12 ± 9	12 ± 2	3.4 ± 1.3	2.4 ± 1.4	1.0 ± 0.2	0.20 ± 0.03	0.17 ± 0.09	0.03 ± 0.05
	Wet	18 ± 2	11 ± 4	10 ± 2	3.6 ± 0.2	2.5 ± 0.8	1.1 ± 0.6	0.14 ± 0.03	0.12 ± 0.05	0.02 ± 0.01
	Early dry	21 ± 2	12 ± 3	9 ± 1	3.6 ± 0.5	2.7 ± 0.7	0.9 ± 0.2	0.21 ± 0.02	0.19 ± 0.05	0.01 ± 0.03
2	Late dry	25 ± 3	14 ± 4	11 ± 1	4.7 ± 0.7	3.6 ± 0.9	1.1 ± 0.2	0.20 ± 0.02	0.18 ± 0.07	0.02 ± 0.06
	Wet	15 ± 3	8 ± 5	7 ± 2	3.0 ± 0.2	2.0 ± 0.5	1.0 ± 0.3	0.13 ± 0.04	0.12 ± 0.11	0.01 ± 0.07
	Early dry	16 ± 3	7 ± 5	8 ± 1	2.6 ± 1.4	2.0 ± 1.8	0.6 ± 0.4	0.13 ± 0.02	0.12 ± 0.05	0.01 ± 0.03
3	Late dry	39 ± 3	29 ± 6	10 ± 3	5.6 ± 0.3	4.9 ± 1.2	0.7 ± 0.9	0.38 ± 0.06	0.35 ± 0.16	0.03 ± 0.10
	Wet	27 ± 2	17 ± 3	9 ± 2	5.1 ± 0.6	4.2 ± 0.9	0.9 ± 0.2	0.23 ± 0.03	0.21 ± 0.04	0.02 ± 0.02
	Early dry	21 ± 2	12 ± 3	9 ± 1	3.8 ± 0.4	2.8 ± 0.9	1.0 ± 0.5	0.18 ± 0.04	0.17 ± 0.06	0.01 ± 0.02

b)

Station	Season	DOC μmol L^{-1}	B-DOC μmol L^{-1}	R-DOC μmol L^{-1}	DON μmol L^{-1}	B-DON μmol L^{-1}	R-DON μmol L^{-1}	DOP μmol L^{-1}	B-DOP μmol L^{-1}	R-DOP μmol L^{-1}
1	Late dry	74 ± 1	12 ± 5	61 ± 4	5.5 ± 0.7	1.8 ± 1.3	3.7 ± 0.6	0.22 ± 0.01	0.15 ± 0.06	0.07 ± 0.05
	Wet	84 ± 2	21 ± 4	63 ± 2	6.2 ± 1.0	2.5 ± 1.3	3.7 ± 0.3	0.28 ± 0.04	0.21 ± 0.07	0.07 ± 0.04
	Early dry	74 ± 1	12 ± 3	62 ± 2	6.0 ± 0.4	2.0 ± 0.5	4.0 ± 0.1	0.25 ± 0.02	0.16 ± 0.08	0.08 ± 0.06
2	Late dry	57 ± 1	6 ± 5	51 ± 4	4.7 ± 0.3	1.5 ± 0.5	3.2 ± 0.3	0.16 ± 0.05	0.09 ± 0.08	0.07 ± 0.04
	Wet	75 ± 3	15 ± 5	61 ± 1	5.0 ± 0.4	1.7 ± 0.8	3.3 ± 0.4	0.21 ± 0.02	0.16 ± 0.08	0.05 ± 0.06
	Early dry	80 ± 1	18 ± 2	61 ± 1	6.0 ± 0.6	2.0 ± 0.9	4.0 ± 0.3	0.25 ± 0.04	0.17 ± 0.06	0.08 ± 0.02
3	Late dry	75 ± 2	8 ± 3	67 ± 1	5.6 ± 1.0	1.5 ± 1.4	4.1 ± 0.4	0.24 ± 0.03	0.14 ± 0.06	0.09 ± 0.04
	Wet	80 ± 1	11 ± 4	69 ± 2	5.7 ± 0.4	1.6 ± 0.5	4.0 ± 0.1	0.21 ± 0.01	0.13 ± 0.02	0.08 ± 0.01
	Early dry	76 ± 1	10 ± 2	67 ± 1	6.2 ± 0.7	1.9 ± 1.2	4.5 ± 0.5	0.23 ± 0.05	0.19 ± 0.15	0.04 ± 0.04

1077 **Table 3.** Matrix of the correlation coefficient (R^2) of the significant ($p < 0.05$) linear

1078 regressions between DOM bioavailability and environmental parameters.

X/Y	BDOC	BDON	BDOP
Chl *a*	0.48*	0.60*	0.79*
DIN	0.58	0.70	0.34
DIP	0.60	0.93	0.73

*Data from station 3 in February 2015 have been omitted to reach significant levels.

1079

1080 **Table 4.** Significant regressions between bioavailable DOM, and inorganic nutrients (DIN,
1081 DIP), and total and bioavailable POM and DOM, and the degradation rate constants. Slope,
1082 intercept, and standard error are values found by Model II regression. R^2 = coefficient of
1083 determination, p = significant levels and n.s. – not significant. In all cases the number of
1084 observations (n) equals 9.

Eq.	X	Y	Slope (±SE)	Intercept (±SE)	R^2	p
1	B-DON	DIN	-0.19 ± 0.05	0.49 ± 0.07	0.70	<0.005
2	B-DOP	DIP	-0.54 ± 0.12	0.16 ± 0.02	0.73	<0.004
3	B-POC	POC	1.1 ± 0.1	8 ± 1	0.96	<0.0002
4	B-PN	PON	1.0 ± 0.1	0.9 ± 0.2	0.98	<0.0001
5	B-PP	POP	1.1 ± 0.1	0.01 ± 0.01	0.99	<0.0001
6	B-DOC	DOC	1.6 ± 0.6	55 ± 5	0.53	<0.03
7	B-DON	DON	1.2 ± 0.6	3.4 ± 0.8	0.52	<0.02
8	B-DOP	DOP	1.0 ± 0.2	0.07 ± 0.03	0.77	<0.002
9	k_{PN}	k_{POC}	0.86 ± 0.23	n.s	0.76	<0.005
10	k_{PP}	k_{POC}	0.73 ± 0.26	n.s	0.65	<0.02
11	k_{PP}	k_{PN}	0.85 ± 0.27	n.s	0.61	<0.02
12	k_{DON}	k_{DOC}	0.82 ± 0.11	n.s	0.87	<0.0003
13	k_{DOP}	k_{DOC}	0.55 ± 0.06	n.s	0.94	<0.0001
14	k_{DOP}	k_{DON}	0.67 ± 0.15	n.s	0.83	<0.001
15	B-POC	k_{POC}	$(6 \pm 2) \times 10^{-3}$	0.16 ± 0.02	0.58	<0.02
16	B-PN	k_{PN}	0.13 ± 0.03	0.18 ± 0.03	0.55	<0.03
17	B-PP	k_{PP}	2.8 ± 0.3	0.23 ± 0.03	0.59	<0.02
18	B-DOC	k_{DOC}	$(10 \pm 2) \times 10^{-3}$	n.s	0.73	<0.004
19	B-DON	k_{DON}	0.09 ± 0.08	n.s	0.50	<0.04
20	B-DOP	k_{DOP}	1.6 ± 0.4	n.s	0.78	<0.002

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Table 5. Degradation rate constants (± standard error) obtained by fitting the exponential decay model to the decrease in carbon, nitrogen and phosphorus in the a) particulate (k_{POC}, k_{PON} and k_{POP}) and b) dissolved organic matter pools (k_{DOC},k_{DON} and k_{DOP}). R^2 = coefficient of determination. In all cases the number of point (n) equals 5.

a)

Station	Season	k_{POC} (day^{-1})	R^2	k_{PON} (day^{-1})	R^2	k_{POP} (day^{-1})	R^2
1	Late dry	0.20 ± 0.06	0.91	0.26 ± 0.05	0.97	0.28 ± 0.09	0.87
	Wet	0.25 ± 0.01	0.93	0.31 ± 0.06	0.96	0.35 ± 0.20	0.90
	Early dry	0.25 ± 0.09	0.87	0.30 ± 0.02	0.98	0.34 ± 0.04	0.98
2	Late dry	0.22 ± 0.03	0.97	0.27 ± 0.03	0.98	0.32 ± 0.03	0.98
	Wet	0.21 ± 0.03	0.98	0.24 ± 0.04	0.97	0.29 ± 0.10	0.87
	Early dry	0.25 ± 0.03	0.98	0.26 ± 0.06	0.94	0.30 ± 0.02	0.98
3	Late dry	0.33 ± 0.07	0.93	0.36 ± 0.04	0.98	0.42 ± 0.10	0.91
	Wet	0.24 ± 0.02	0.96	0.32 ± 0.03	0.98	0.35 ± 0.10	0.86
	Early dry	0.22 ± 0.04	0.97	0.26 ± 0.06	0.91	0.36 ± 0.01	0.96

b)

Station	Season	k_{DOC} (day^{-1})	R^2	k_{DON} (day^{-1})	R^2	k_{DOP} (day^{-1})	R^2
1	Late dry	0.13 ± 0.03	0.91	0.21 ± 0.09	0.84	0.26 ± 0.11	0.92
	Wet	0.20 ± 0.06	0.89	0.25 ± 0.07	0.90	0.33 ± 0.08	0.94
	Early dry	0.17 ± 0.06	0.84	0.22 ± 0.08	0.76	0.30 ± 0.06	0.93
2	Late dry	0.04 ± 0.01	0.89	0.05 ± 0.01	0.94	0.09 ± 0.02	0.94
	Wet	0.17 ± 0.05	0.87	0.24 ± 0.09	0.87	0.28 ± 0.01	0.96
	Early dry	0.19 ± 0.03	0.97	0.20 ± 0.05	0.93	0.33 ± 0.04	0.92
3	Late dry	0.11 ± 0.01	0.88	0.12 ± 0.02	0.98	0.23 ± 0.07	0.87
	Wet	0.15 ± 0.02	0.98	0.18 ± 0.05	0.90	0.25 ± 0.03	0.89
	Early dry	0.15 ± 0.04	0.85	0.20 ± 0.06	0.86	0.28 ± 0.04	0.98

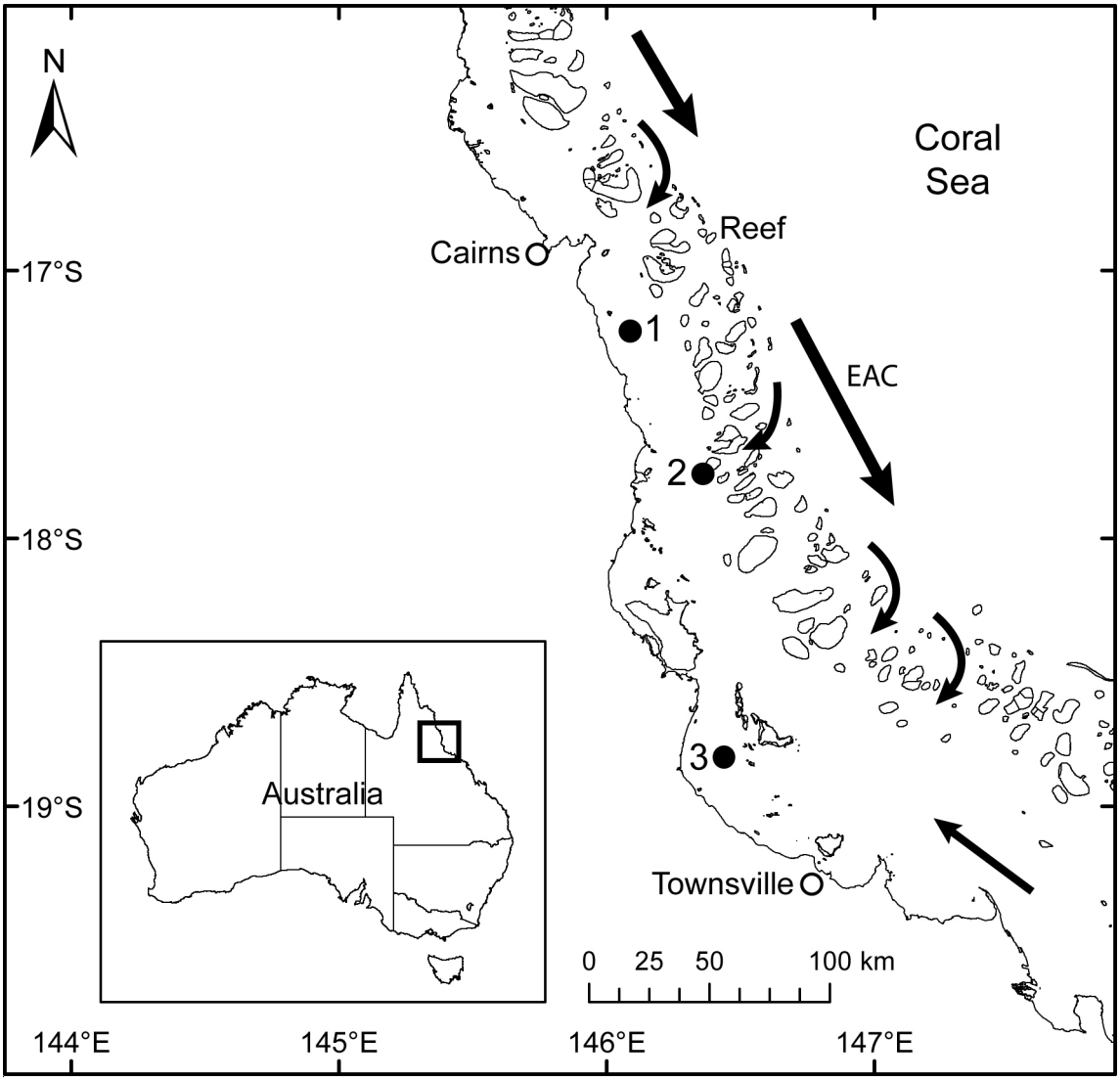
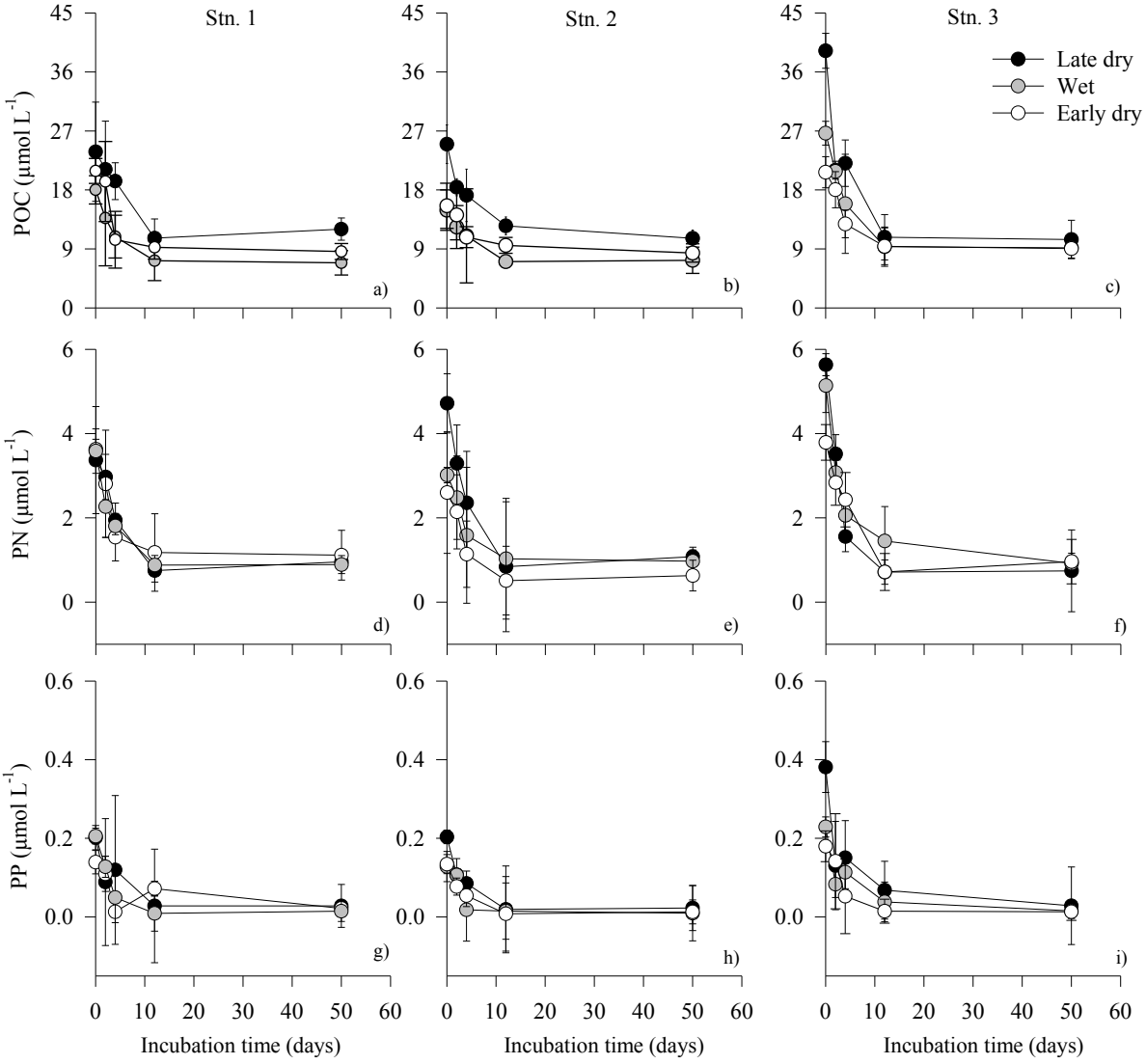


Fig. 1. Lønborg et al.



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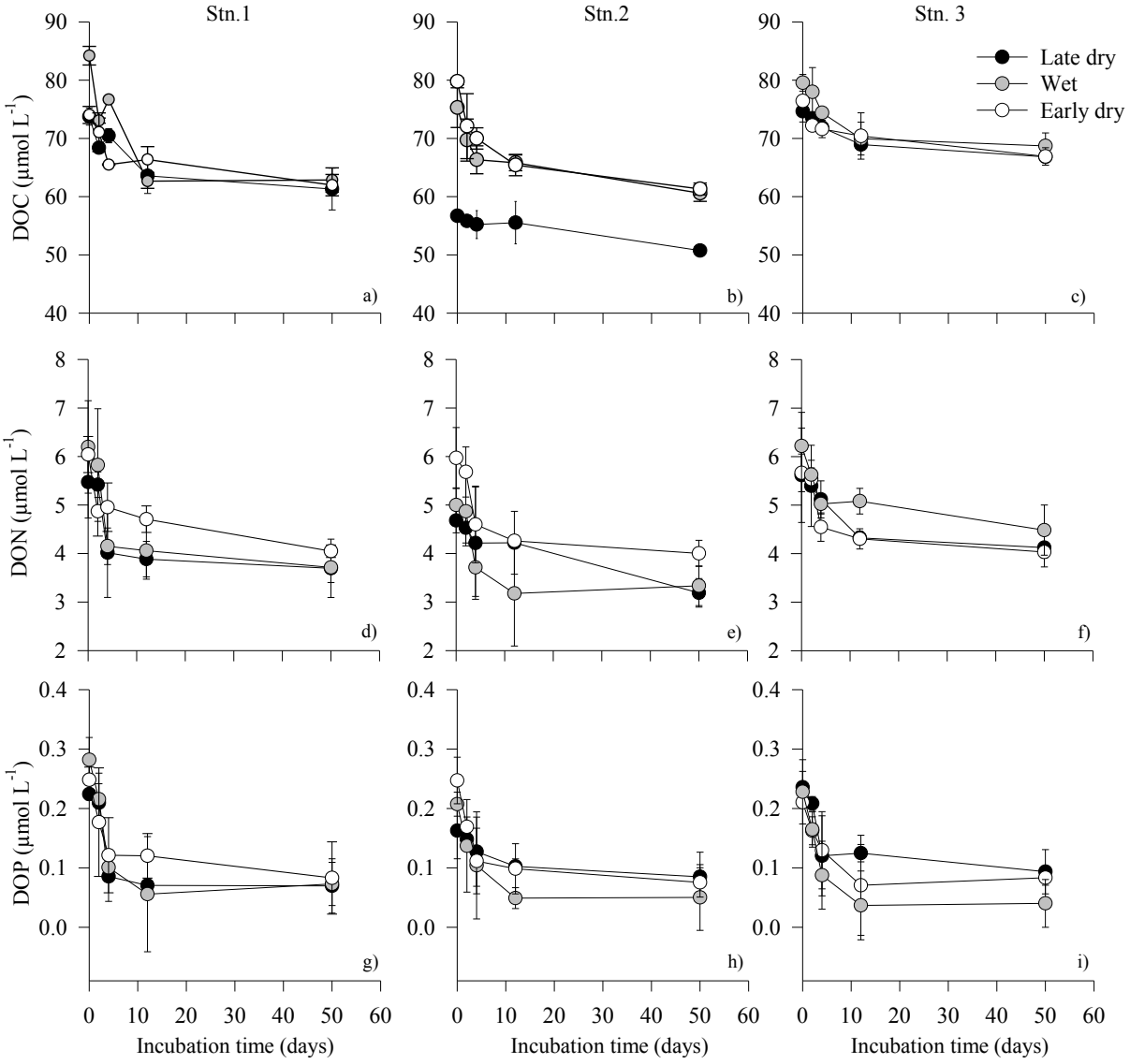
1094 **Fig. 2.** Lønborg et al.



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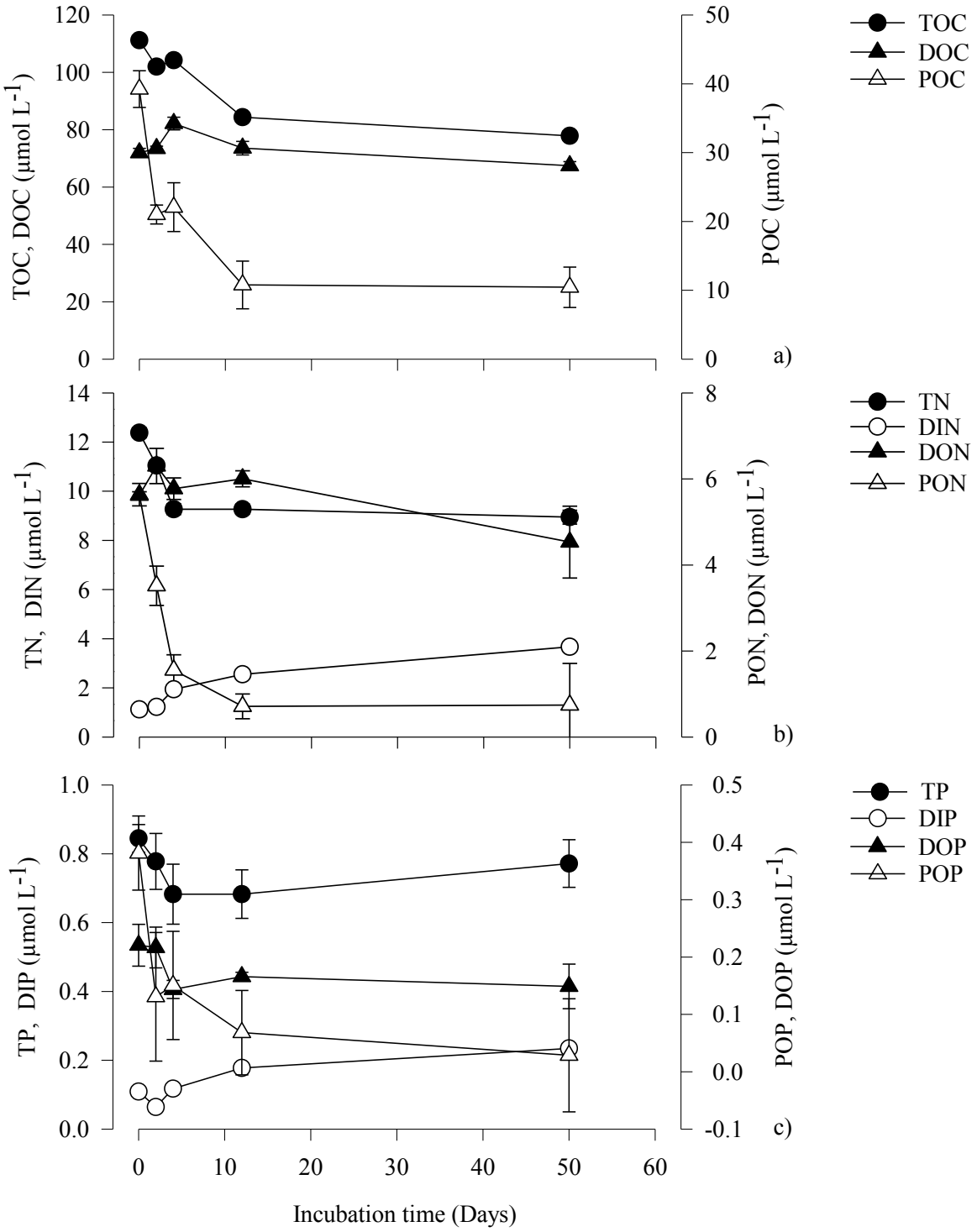
1096 **Fig. 3.** Lønborg et al.



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1098 **Fig. 4.** Lønborg et al.

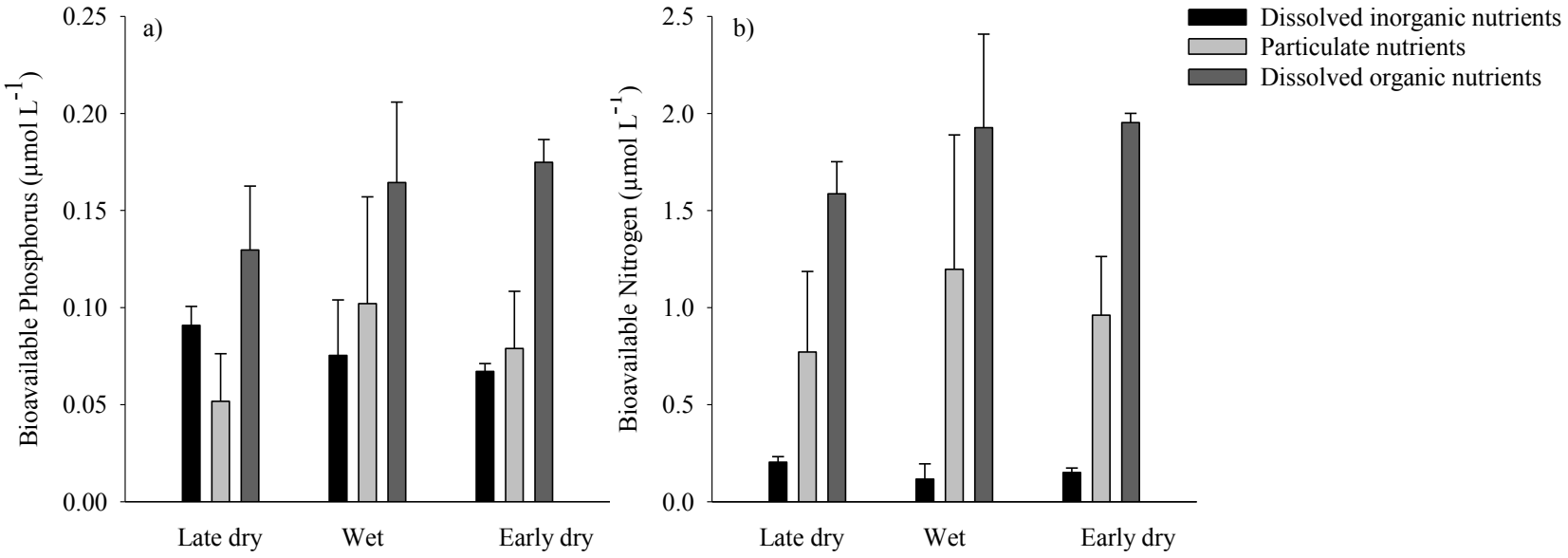

Fig. 5. Lønborg et al.

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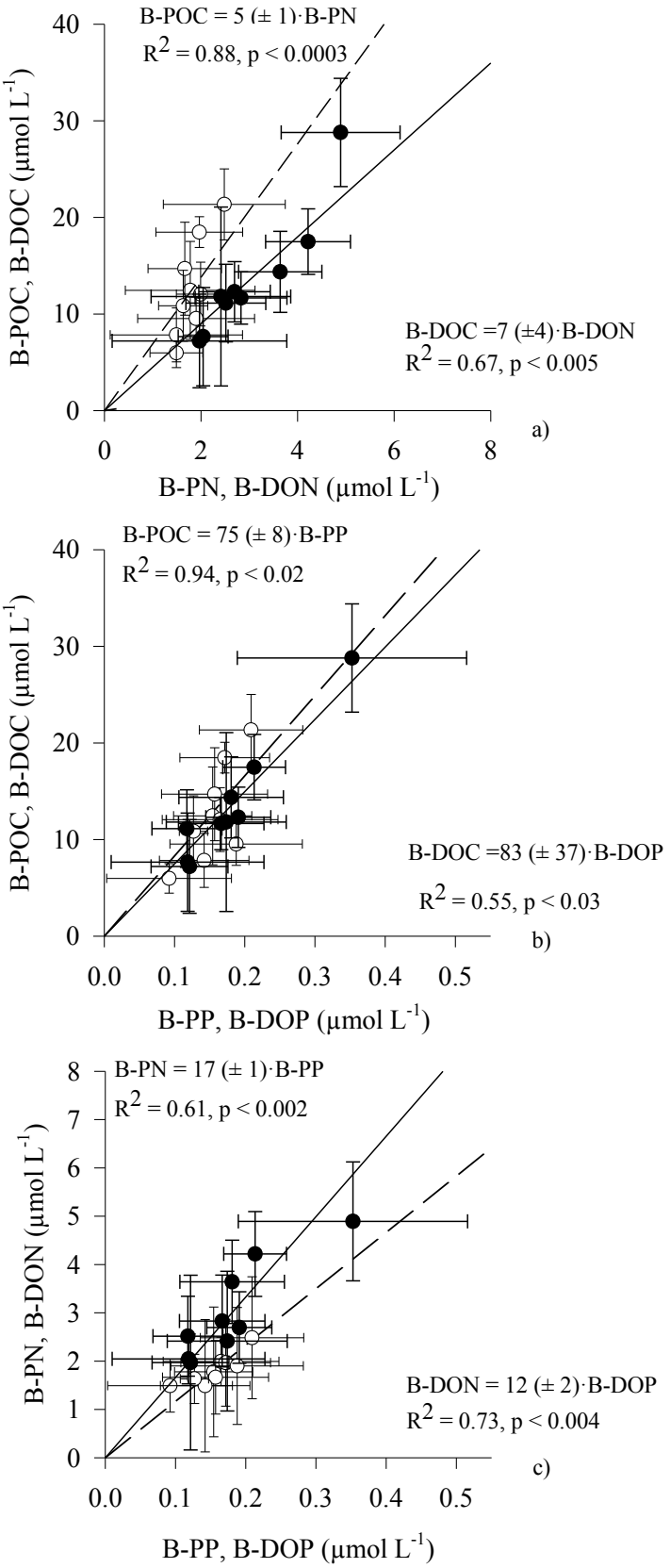

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1103 **Fig. 6.** Lønborg et al.